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Nutrient competition between phytoplankton species in multispecies chemostat experiments

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With 4 figures and 2 tables in the text

Abstract

Natural phytoplankton from Lake Constance was exposed to competition experiments in chemostat cultures at 6 different Si : P ratios. As predicted from theoretical considerations, competitive exclusion of all but one species occurred when all species were limited by the same nutrient. Coexistence in equilibrium occurred when the coexisting species were limited by different resources. Duplicate experiments with similar nutrient conditions, but different inoculum composition, yielded identical final equilibria. There was a logical pattern over the whole range of experimental conditions, with increasing importance of diatoms at increasing Si : P ratios. Comparability with lake observations is discussed.

Introduction

Depletion of mineral nutrients for algal growth during the summer period is a common feature in stratified lakes. Consequently competition for limiting nutrients becomes an important factor in phytoplankton species succession. According to classical ecological theory, increasing competition for a common resource must lead to competitive exclusion of all species but the one most efficient in the utilization of low concentrations ("principle of competitive exclusion", Hardin 1960). Nevertheless numerous species of phytoplankton coexist even during extremely nutrient depleted periods in natural lakes ("paradox of the plankton", Hutchinson 1961). Several concepts have been proposed to solve this paradox. Hutchinson (1961) himself suggested that competitive exclusion will not be achieved, if the time required for competitive exclusion is longer than the time of persistence of environmental conditions that favour one particular species. Richerson, Armstrong & Goldman (1970) have extended the concept of disequilibrium by emphasizing spatial heterogeneity in phytoplankton distribution. In contrast to these concepts Petersen (1975), Taylor & Williams (1976), and Tilman (1977) have analyzed the possibilities of coexistence in steady state equilibrium as it can be experimentally realized by the chemostat culture. Since the theory and the technique of the chemostat have been explained by Müller (1972), it shall not be repeated in detail. According to Monod (1950) the steady state relationship between the growth

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rate (μ) and the concentration of a limiting nutrient (S) can be expressed by a Michaelis-Menten type of equation:

$$\mu = \frac{\mu_{max} \cdot S}{S + k_s} \qquad \text{equ. 1}$$

where k_s is the half saturation constant. k_s and μ_{max} are considered species specific constants for given physical (temperature, light) conditions. If two species are grown in the same chemostat limited by the same nutrient, species 1 will replace species 2 if the following conditions are fulfilled:

$$\frac{k_{s1}}{\mu_{max_1} - D} < \frac{k_{s2}}{\mu_{max_2} - D} \qquad \text{equ. 2}$$

where D is the dilution rate of the culture. Only when the above expression is equal for both species ("neutral equilibrium") will competitive exclusion not occur. When different species are limited by different resources coexistence in equilibrium is possible. TILMAN (1977) has tested this concept with *Asterionella formosa* HASS. and *Cyclotella meneghiniana* KÜTZ. and phosphate and silicate as potentially limiting nutrients. At a molar ratio of Si : P below 6 : 1, growth of both species was silicate-limited and *Cyclotella* outcompeted *Asterionella*; at Si : P from 6 : 1 to 90 : 1 *Asterionella* was silicate-limited and *Cyclotella* phosphate-limited and both species coexisted in steady state; at Si : P above 90 : 1 both species were phosphate limited and *Asterionella* was the successful competitor. Equilibrium species composition perfectly followed the theoretical prediction derived from the Michaelis-Menten parameters of both species, which had previously been assessed in monocultures.

I have attempted to extend TILMAN's approach to a natural assemblage of phytoplankton, by which two additional complications have been added to the experimental design: (I) The inoculum out of which the successful competitors were selected consisted of more than thirty species with unknown physiological parameters instead of two species with well defined Michaelis-Menten constants. (II) The experiments could not be carried out simultaneously, only successively. Therefore the relative abundance of species in the inoculum varied from experiment to experiment. (III) Instead of a direct transition from the inoculum to the equilibrium species composition in two-species experiments a more or less complicated species succession could be expected. Since phosphate and silicate are the only macronutrients that are depleted down to limiting levels during the vegetation period of Lake Constance (ELSTER 1982; MOHAMMED & MÜLLER 1981; SOMMER 1981 b; STABEL & TILZER 1981), they were chosen as potentially limiting nutrients.

The following questions should be answered by the experiments:

I. Is there a regular pattern in the species succession during the course of the experiments?

II. Can competitive exclusion of all but one (in the case of single nutrient limitation) or two (in the case of double nutrient limitation) species be achieved, even if the inoculum consists of numerous species.
III. Is the result of competition experiments predictable at the species level or only at a more general level (e. g. diatoms, green algae, ...).
IV. Is the replication of experiments with similar nutrient conditions spoiled by differences in the inoculum; or are the results independent of the inoculum species composition?
V. Can the results be compared to real lake situations?

Methods

Algae were grown in a 20 l Biolafitte-Methrom chemostat. The inoculum consisted of 10 l of natural phytoplankton suspension taken from the light saturated layer of Lake Constance at the beginning of each experiment. Before being filled into the culture vessel the plankton suspension was bubbled for 1 h by nitrogen in order to kill zooplankton by oxygen depletion. The dilution rate was $0.3\,d^{-1}$; temperature was 18 °C and surface light intensity was $1.6 \cdot 10^{16}$ quanta $\cdot\, cm^{-2}s^{-1}$. Tests with doubled and halved light intensities indicated light saturation at least for the four species that turned out as competively superior in the experiments. pH was regulated to 7.0 by addition of CO_2 in order to prevent carbon limitation. The nutrient solution was CHU 12 as modified by MÜLLER (1972), with all other nutrients in excess in comparison to phosphate and silicate. The concentration of PO_4—P was $75\,\mu g \cdot l^{-1}$, the concentration of silicate was varied between experiments. Six different Si : P ratios were used: 4 : 1, 10 : 1, 20 : 1, 30 : 1, 40 : 1, 80 : 1, which translates to absolute concentrations of dissolved silicon of 270, 675, 1350, 2025, 2700 and 5400 $\mu g\ Si \cdot l^{-1}$.

Each experiment was duplicated with as much difference in the inoculum species composition as possible in order to analyze the effect of the inoculum.

Samples for cell-counts and dissolved nutrient analysis were taken daily. Cell-counts were performed according to UTERMÖHL's inverted microscope technique. 400 individuals per species were counted, thus giving a counting accuracy of roughly ± 10 %. Algal biomass was estimated as cell volume, for which the linear dimensions of 50 cells of each species were taken. Geometrial calculation of the volumes followed the recommendations of ROTT (1981). Samples for dissolved nutrient analysis were filtered through 0.2 μm pore size membrane filters and analysed with the help of a Technicon-autoanalyzer. Analysis of dissolved silicon was performed according to STRICKLAND & PARSONS (1968) and soluble reactive phosphorus was measured according to VOGLER (1965).

Even if a species completely stops growth, disappearance from the culture by dilution is an asymptotic process. Therefore an artificial limit was set, at which competitive equilibrium was considered to be achieved. Experiments were ended, when the successful species or combination of species comprised at least 95 % of total biomass and all other species decreased in population density continuously for more than two dilution periods (6⅔ days).

Results

All experiments had a typical time course that consisted of three phases (Fig. 1): A start phase (I) where species, that were already dominant in the in-

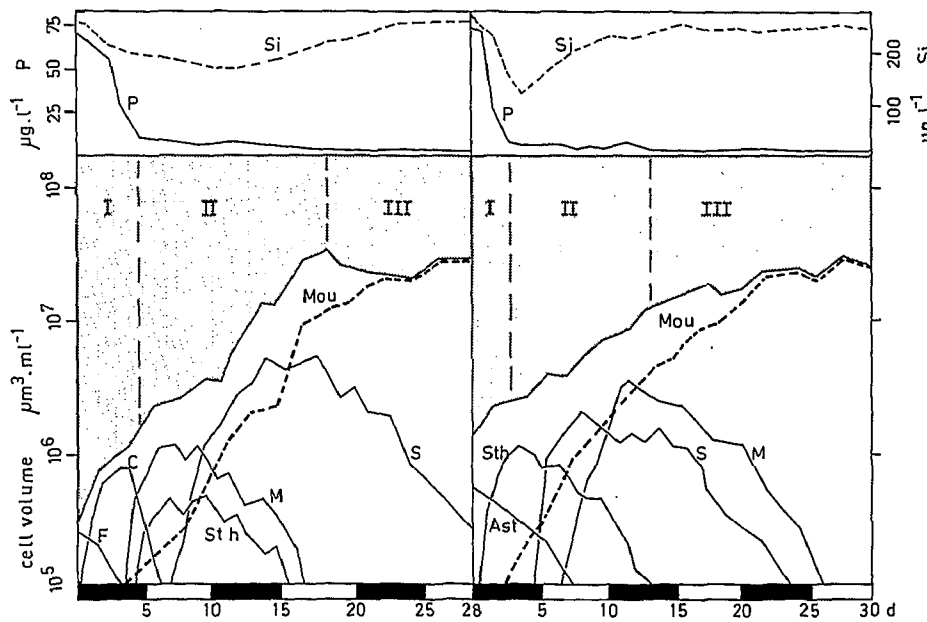

Fig. 1 a. Si : P in the inflow 4 : 1.

Fig. 1. Time course of competition experiments: upper section: dissolved nutrient concentration (Si and P in $\mu g \cdot l^{-1}$) in the cultures. Lower section: total biomass and biomass of dominant algal species. (cell volume in μm^3 ml^{-1}; log-scale). Thick broken lines: ultimate dominant species.

Abbreviations: Ast: *Asterionella formosa*, C: *Chlorella* sp. cr: *Cryptomonas ovata*, F: *Fragilaria crotonensis*, G: *Golenkiniopsis solitaria*, Kol: *Koliella spiculiformis*, M: *Monoraphidium contortum*, Mou: *Mougeotia thylespora*, N: *Nitzschia actinastroides*, P: *Pandorina morum*, R: *Rhodomonas minuta*, S: *Scenedesmus*, Sta: *Stephanodiscus astraea*, Sth: *Stephanodiscus hantzschii*, Syn: *Synedra acus*.

oculum or just about to bloom in the lake, dominated. A transition phase (II), during which a succession of several species could be observed, but which later disappeared from the cultures, and a final phase (III), which was characterized by asymptotic approach to steady state equilibrium.

The start phase

Mixing 10 l of nutrient solution with 10 l of original lake plankton offered nutrient-saturated conditions to all species. After a short lag phase of one to three days vigorous growth of all species started. The species composition paralleled the on-going development in the lake. If the growth rates are corrected for losses by dilution they should be close to μ_{max}. Because μ_{max} by definition applies to monocultures, the growth rates achieved in phase I of the experiments shall be defined as "initial growth rate" (μ_o). There was good agreement between the different experiments for a given species, as can be seen

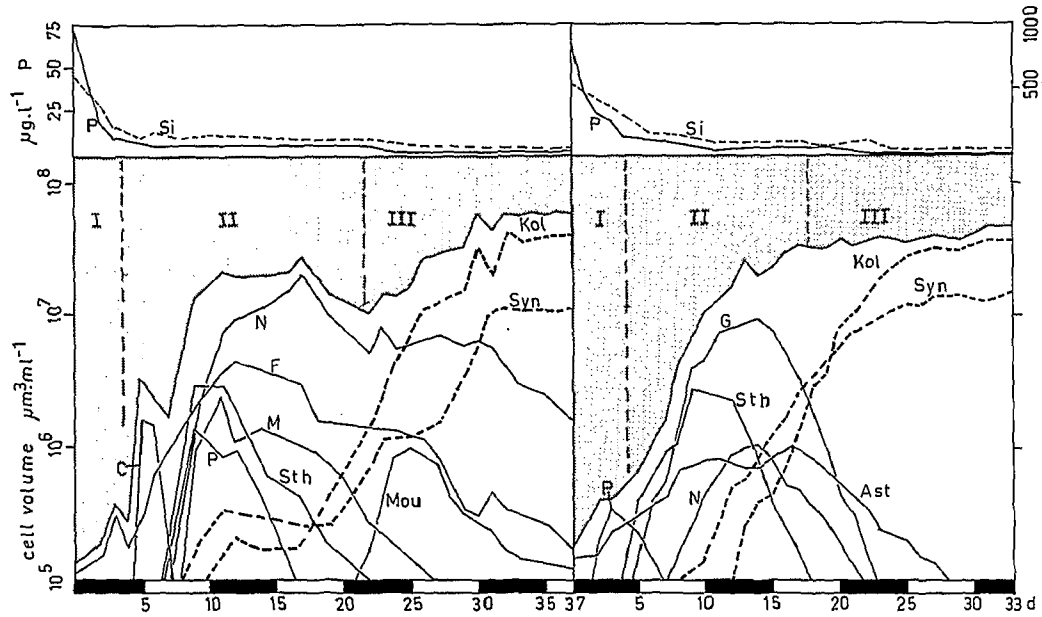

Fig. 1b. Si:P in the inflow 10:1.

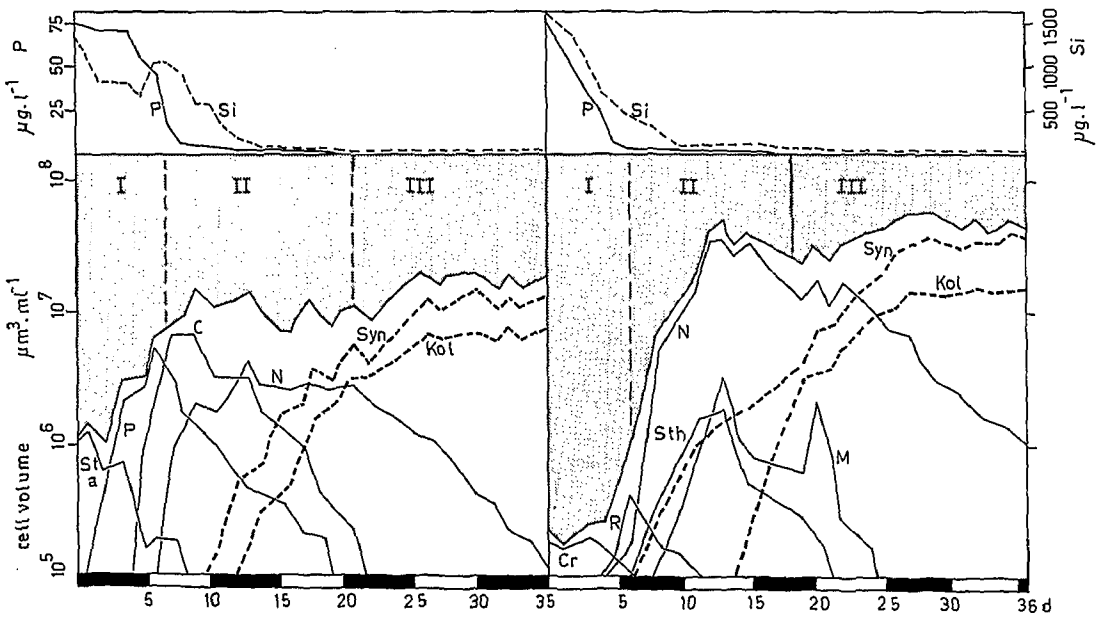

Fig. 1c. Si:P in the inflow 20:1.

from the narrow standard deviation in Table 1. The initial growth rates observed here were in the same range as values for the maximum growth rate available from the literature. Surprisingly low initial growth rates were found for *Cryptomonas ovata* EHR., *C. marssonii* SKUJA, *Rhodomonas minuta* SKUJA,

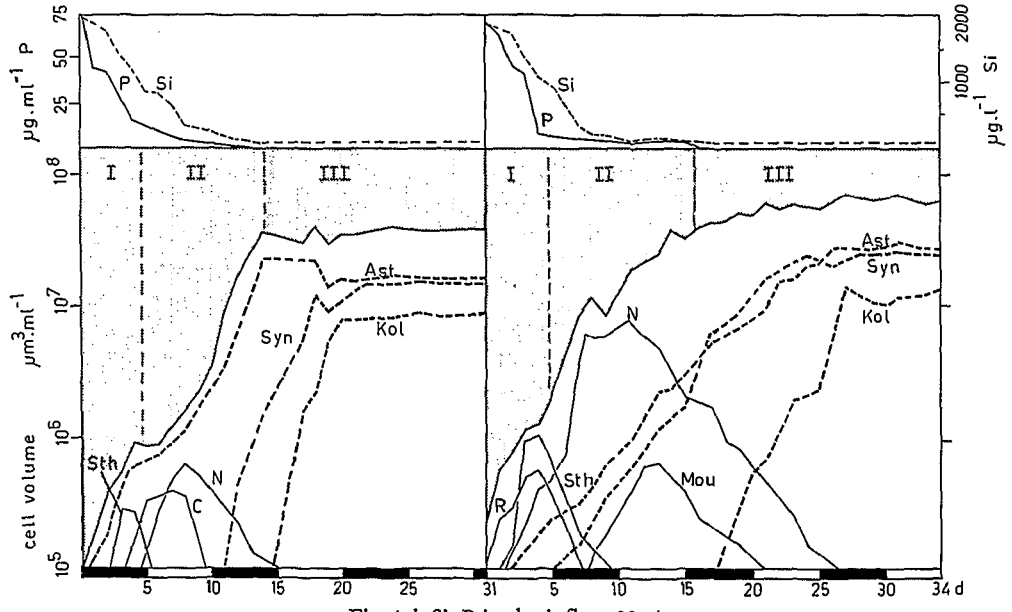

Fig. 1 d. Si : P in the inflow 30 : 1.

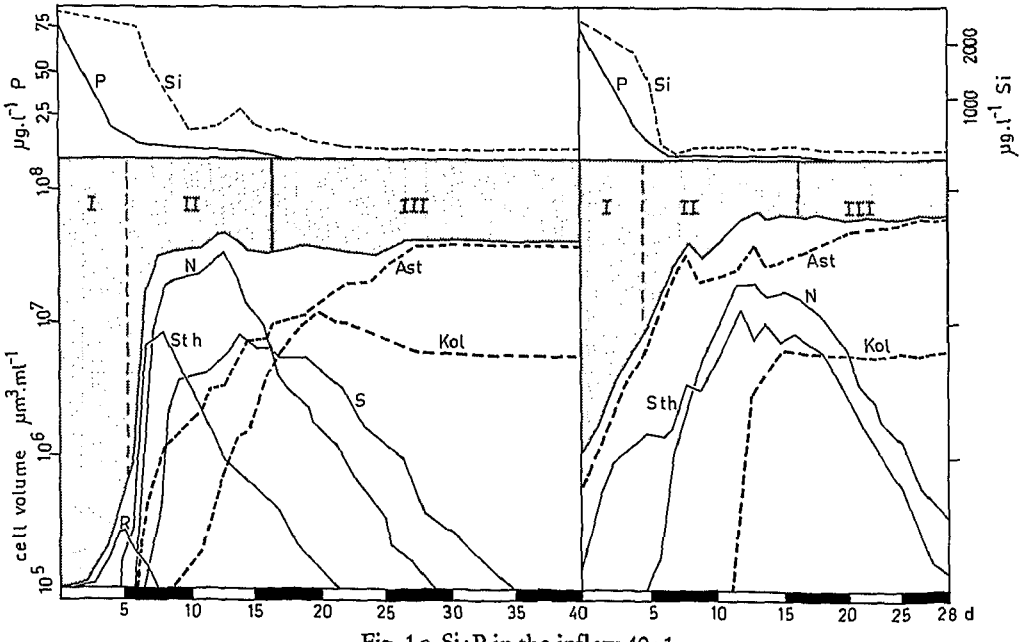

Fig. 1 e. Si : P in the inflow 40 : 1.

R. lens Pascher & Ruttner, which are among the fastest growing species in the lake itself (Sommer 1981). It is likely that these naked flagellates are handicapped by a lower resistance against mechanical stirring of the cultures in com-

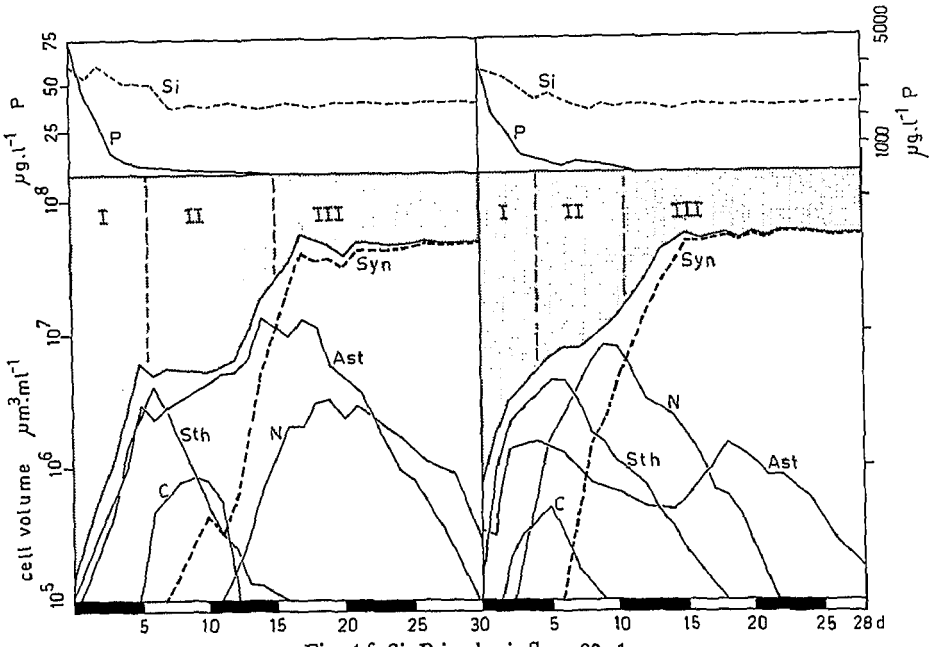

Fig. 1 f. Si:P in the inflow 80:1.

parison to algae with cell walls. In the case of the other species, interspecific comparison of μ_o has yielded parallel results to interspecific comparison of net rates of increase (k) in Lake Constance (SOMMER 1981 a). There is a negative correlation between cell-size (or colony-size in the case of compact colonial forms) and the initial growth rate. Regressions were calculated for all coccale algae and for diatoms and chlorococcales separately.

The overall regression can be expressed by the equation (together with 95% confidence limits):

$$\mu_o[d^{-1}] = 2.8\,(\pm\,0.24) - 0.22\,(\pm\,0.04).\log^{10} V[\mu m^3] \qquad \text{equ. 3}$$

The regression lines valid for diatoms and chlorococcales separately lie within the confidence limits of equ. 3 (Fig. 2). Therefore, size-dependence in the variation of μ_o is more important than taxonomic differences, which is in agreement with the findings of BANSE (1976). As it has been observed in the lake itself, the rule of negative correlation between cell-size and growth-rate does not apply to flagellates, especially in the case of large *Pandorina morum* BORY, which is among the most rapidly growing species.

The transition phase

After several days of cultivation concentrations of dissolved phosphorus decreased to 4 to 10 $\mu g \cdot l^{-1}$. Growth rates of algae were now already markedly below the initial growth rates and total phytoplankton biomass near the level

Table 1. Initial growth rate (μ_o in ln – units per day) of algal species in comparison to cell volume (μm^3) and literature data for μ_{max}.

	μm^3	μ_o (number of experiments)	μ_{max} (literature)	
Diatoms				
Stephanodiscus hantzschii	50	1.91±0.25(10)		
Nitzschia actinastroides	200	1.80±0.16(12)	2.06(1)	1.87(2)
Stephanodiscus binderanus	300	1.54±0.13(10)		
Fragilaria capucina	350	1.55±0.12(8)	1.82(2)	
Melosira granulata	500	1.34±0.16(8)		
Asterionella formosa	700	1.34±0.16(12)	1.3–1.7(1)	0.76(3)
Fragilaria crotonensis	1,000	1.21±0.19(11)	1.39(2)	
Synedra acus	1,400	1.11±0.13(10)	1.51(2)	
Stephanodiscus astraea	4,000	0.84±0.13(7)		
Chlorococcales and unicellular **Ulotrichales**				
Chlorella sp.	4	2.19±0.34(11)	1.8–4.9(1)	
Koliella spiculiformis	30	2.02±0.30(9)		
Monoraphidium contortum	30	2.00±0.15(10)		
Scenedesmus quadricauda	350	1.80±0.10(10)		
Scenedesmus opoliensis	500	1.68±0.20(6)		
Oocystis marssonii	1,200	1.39±0.20(5)		
Pediastrum duplex	4,000*	0.80±0.15(6)		
Pediastrum boryanum	8,000*	0.69±0.18(6)		
Coelastrum reticulatum	14,000*	0.45±0.18(5)		
Others				
Chlamydomonas sp. I	400	2.08±0.20(7)		
Chlamydomonas sp. II	1,500	1.75±0.30(5)		
Pandorina morum	18,000*	1.64±0.30(10)		
Mougeotia thylespora	2,000	1.22±0.20(11)		
*Cryptomonas ovata***	2,000	0.84±0.20(8)		
*Cryptomonas marssonii***	600	0.69±0.15(6)		
*Rhodomonas lens***	300	0.65±0.13(7)		
*Rhodomonas minuta***	80	0.88±0.11(9)		

1. Jørgensen 1979, 2. Müller 1972, 3. Tilman & Kilham 1976, 4. Mur, Gons & van Liere 1978.

* colony size.

** species probably handicapped by mechanical stress.

of the final equilibrium. There was a series of mass developments of several algal species without any regular pattern in temporal sequence (Fig. 1). Dominant species in this phase belonged either to Chlorophyceae or diatoms: *Chlorella* sp., *Scenedesmus quadricauda* Brebisson, *Monoraphidium contortum* Komarkova, *Golenkiniopsis solitaria* Korch., *Stephanodiscus hantzschii* Grun., *Nitzschia actinastroides* V. Goor, *Pandorina morum* Bory. All were species, that had achieved high initial growth rates ($> 1.6\,d^{-1}$) during phase I. Their

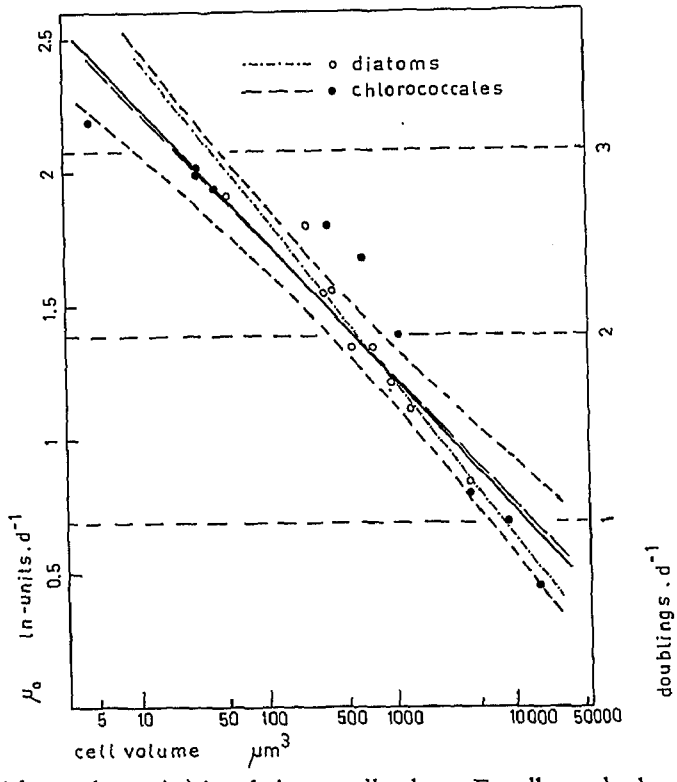

Fig. 2. Initial growth rate (μ_o) in relation to cell volume. For all coccale algae solid line and 95 % confidence limit (broken line):

$$\mu_o = 2.8\ (\pm\ 2.4) - 0.22\ (\pm\ 0.04) \cdot \log^{10} V;\ r = 0.95$$

for diatoms:

$$\mu_o = 3.04\ (\pm\ 0.34) - 0.26\ (\pm\ 0.07) \cdot \log^{10} V;\ r = 0.98$$

for chlorococcales:

$$\mu_o = 2.76\ (\pm\ 0.39) - 0.22\ (\pm\ 0.06) \cdot \log^{10} V;\ r = 0.95.$$

ability to grow rapidly enabled them to surpass species that had been more abundant in the inoculum. With the exception of *Pandorina morum* they were all small algae. Phase II can be characterized by r-selection sensu KILHAM & KILHAM (1980): high growth rate, commonly associated with small body size, is the predominant selective advantage, and competition for resources plays no important role.

The final equilibrium

With increasing nutrient depletion the abundance of the species of phase II decreased and the phytoplankton community approached its final composition. Throughout the whole range of experiments only 4 species could establish themselves in the steady state assemblage: *Mougeotia thylespora* SKUJA (Zygnematales), *Koliella spiculiformis* HINDAK (Ulotrichales) and the pennate

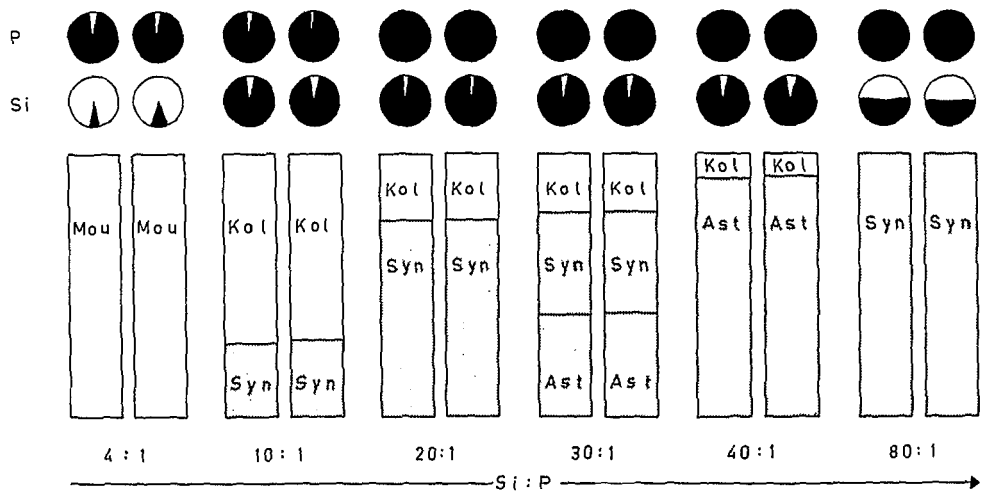

Fig. 3. Final equilibrium conditions in competition experiments.
Species composition: vertical bars, Ast: *Asterionella formosa*, Kol: *Koliella spiculiformis*, Mou: *Mougeotia thylespora*, Syn: *Synedra acus*. Nutrient conditions: circles, black: consumed; white: unconsumed, i.e. still dissolved in cultures.

diatoms *Synedra acus* KÜTZ. and *Asterionella formosa* (Fig. 3). In the experiments with a nutrient ratio of Si:P from 4:1 to 40:1, both nutrients were depleted to more than 90%, indicating double limitation that led to coexistence of two, at Si:P = 30:1 three species in the steady state phase. At Si:P = 80:1 nearly half to the silicate remained unused in the dissolved phase, here phosphorus was limiting for all species and *Synedra acus* turned out to be the most successful competitor. At the lowest silicate concentration (Si:P = 4:1) all diatoms were probably so silicate-limited, that they could not withstand the dilution rate and *Mougeotia thylespora* was the most successful competitor among the non-diatom species.

Discussion

Comparison of the experiments

There was no regular pattern in the succession of dominant species before the final equilibrium was reached. Phase I was highly dependent on the inoculum; during phase II only a few species became dominant in terms of biomass, but the time sequence of their maxima was not the same in the experiments. It was controlled both by the abundance in the inoculum and the growth rates achieved. In contrast to the initial and intermediate stages, the final equilibrium was surprisingly regular: duplicate experiments with different inocula but similar nutrient conditions yielded identical final equilibria. Even extreme scarcity of a species (i.e. undetectability, less than 0.1 cells per

ml) in the inoculum did not prevent it from becoming dominant. This has important consequences for the question of perennation of planktonic algae. The four species in the equilibrium phase as well as the dominant species of phase II always seem to be capable of beginning mass growth in the lakes, even if they are not detectable in routine counts.

Comparison of the different experiments leads to the conclusion, that TILMAN's concept of coexistence and competitive exclusion in steady state is not only confined to artificial two-species systems, but also valid for natural assemblages. Contradictory findings by HOLM & ARMSTRONG (1981), in whose two-species experiments with *Asterionella formosa* and *Microcystis aeruginosa* KÜTZ. competitive exclusion was never achieved, can probably be explained by the pulsed nature of their semicontinuous dilution. Theoretical considerations (STEWART & LEWIN 1973) have shown that pulsed dilution can enable coexistence of species competing for the same resource. The equilibrium coexistence of three species (*Koliella spiculiformis, Synedra acus, Asterionella formosa*) at Si:P = 30:1 is considered a "neutral equilibrium" between *Synedra* and *Asterionella* in their competition for silicate, i. e. as the point of intersection of the growth-silicate curves. Further more it is surprising that Synedra is competitively superior to *Asterionella* both at low and at the highest concentrations of silicate, while *Asterionella* is superior at medium concentrations. If growth-nutrient interactions are described by Michaelis-Menten type curves only one point of intersection between the curves of two species should be possible. There may be two explanations: (I) It has been shown both experimentally (MOED 1973) and by analysis of field data (LUND 1950, SOMMER & STABEL 1983) that *Asterionella formosa* is highly affected by cell mortality at limiting concentrations of silicate. If a death-rate which increases with sinking concentrations of silicate is subtracted from the growth-rate as described by the Miachaelis-Menten equation, the resulting curve might have two points of intersection with a growth-silicate curve of a species less or not at all affected by mortality (Fig. 4). (II) When silicate is a surplus factor for both species (Si : P = 80 : 1) both species compete for phosphate, and at lower concentrations of silicate both compete for silicate. *Synedra acus* then should be the better competitor for phosphate and for silicate at low concentrations and *Asterionella formosa* the better competitor for silicate at higher concentrations of silicate.

Comparison between experiments and Lake Constance

Competition for limiting nutrients can only be expected during the summer period (MOHAMMED & MÜLLER 1981; ELSTER 1982) and in some years also during september and october (e. g. in 1979; STABEL & TILZER 1981). Therefore comparison between the lake and the experiments shall only be attempted for this phase. Experimental temperatures and light intensities have

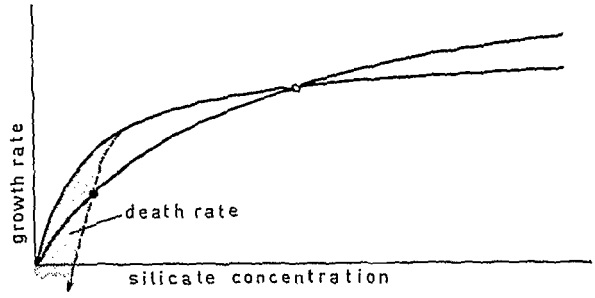

Fig. 4. Hypothetical growth-silicate relationships for two different species: A: lower, maximum growth rate, higher affinity, mortality at low concentration (shaded area). B: higher maximum growth rate, lower affinity, no mortality.
Open circle: point to intersection if only the growth rate is considered; full circle: additional point of intersection, if mortality is also taken into account.

roughly simulated average summer conditions in the light-saturated water layer. If the dependance of species composition on nutrient concentrations is to be analyzed, the appropriate correlate to resource availability is growth and not population density, because maximum density commonly coincides with depletion of the essential resource. For the sake of comparison soluble reactive phosphorus concentrations have been divided into three categories (Table 1): (I) Phosphorus rich conditions with concentrations above 10 μg $P \cdot l^{-1}$. This limit is well above the half saturation constants of the vast majority of species reported in the literature. Algal growth can be considered as phosphorus-saturated and competion for phosphate plays no role in species selection. (II) Moderate concentrations between 2 and 10 μg $P \cdot l^{-1}$. Half saturation constants for many green algae lie in this range (JØRGENSEN 1979). Moderate competition for phosphate might be expected in the lake. (III) Strong phosphorus depletion at concentrations below 2 μg $P \cdot l^{-1}$. This is the range from which half-saturation constants of pennate diatoms (TILMAN & KILHAM 1976) and chrysophyceae (LEHMAN 1976; LEHMAN, BOTKIN & LIKENS 1975) are reported. (IV) The forth category is the combination of phosphate and silicate depletion, which occurs in Lake Constance after mass developments of diatoms. From Table 2 it can be seen that species important during phase II of the experiments grow at rich or moderate phosphate concentrations in the lake. The importance of diatoms during the period of combined phosphate depletion and still high concentrations of silicate is well reflected in their position in the steady phase of the experiments. The transition from a phosphorus-saturated Cryptophyceae/Chlorophyceae to a phosphorus-limited diatom assemblage in early summer is a very regular phenomenon in Lake Constance, that has been observed by the author in 1979, 1980, 1981, 1982. The position of *Mougeotia thylespora* in the experiments (phase III, lowest Si:P ratio) is also in good agreement with its position in

Table 2. Comparison of occurance of phytoplankton species in the experiments and in Lake Constance. Only growing or stable populations habe been taken into account.

Species	Experiments								Lake			
	Phase I	Phase II	Phase III Si:P 4:1	10:1	20:1	30:1	40:1	80:1	P-rich	moderate P-depletion	strong P-depletion	P and Si-depletion
Diatoms												
Stephanodiscus hantzschii	●	●							●	○		
Nitzschia actinastroides	○	●							○	○		
Fragilaria capucina	○	○							○	○		
Stephanodiscus binderanus	●	○							○	○	●	
Melosira granulata	○									○	◑	
Asterionella formosa	●					◑	●				●	
Fragilaria crotonensis	●										●	
Synedra acus	○			◑	◑	◑		●		○	◑	
Stephanodiscus astraea	●								only winter			
Green algae												
Chlorella sp.	○	◑							◑			
Koliella spiculiformis				●	◑	◑	○		?	?		
Monoraphidium contortum		●							○			
Golenkiniopsis solitaria		●							○			
Scenedesmus quadricauda	○	●							○	○		
Scenedesmus opoliensis	○	○							○	○		
Oocystis marssonii	○	○										
Pediastrum duplex	○								○	○	○	○
Pediastrum boryanum	○								○	○	○	○
Coelastrum reticulatum	○								○	○	○	○
Mougeotia thylespora	○		●							○	○	●
Chlamydomonas sp. I	○	◑							◑			
Chlamydomonas sp. II	○	◑							◑			
Pandorina morum	◑	●							●	○		
Cryptophyceae												
Cryptomonas ovata	◑								●	◑		
Cryptomonas marssonii	○								○	○		
Rhodomonas minuta	●								●	○		
Rhodomonas lens	○								●			

● Dominant species, ◑ subdominant (> 10% of total biomass), ○ detactable (> 0.1 cells per ml). Winter and autumn phytoplankton in the lake is not included, because in this strongly light limited phase nutrient competition plays no role.

Lake Constance. For *Koliella spiculiformis* the lake-experiment comparison is difficult because of its scarcity in the lake.

In spite of these encouraging similarities between experimental results and lake observations there are important differences: Many of the phase II-species are unimportant in the Lake Constance phytoplankton community and many of the species important in the lake play no major role in the experiments. This applies for the Cryptophyceae, which are the most important group under phosphorus-saturated conditions in the lake, and for the Dinophyceae and Cyanophyceae, which are typical for the combination of phosphate- and silicate depletion. These differences are due both to technical artifacts of the culture method and to principal differences between competition in continuous culture and phytoplankton succession in the lake. The main technical artifact is the mechanical stress imposed on the algae by stirring of the cultures, which is necessary to prevent wall growth. Especially the naked flagellates *Cryptomonas* and *Rhodomonas* are handicapped by that factor. During their decline in the cultures, they decrease much faster than should be expected from the dilution rate, which indicates considerable cell mortality. The shift from a predominantly Cryptophyceae — diatom competition system with green algae playing only a minor role in the lake to a green algae-diatom system in the experiments is probably the result of this artifact.

In the lake algae are submitted to several loss processes (e. g. grazing, sedimentation, parasitism), that are highly species specific. Conversely, in the competition experiments described here a uniform loss rate (i. e. the dilution rate) is imposed on all species and selective loss factors such as grazing and sedimentation are deliberately excluded. Hence, competition for a limiting resource can be studied without interference from the other factors regulating species succession. It is no surprise, then, that algae that owe their importance in the lake mainly to loss resistance and not to competitive superiority were never important in the course of the experiments. This is probably most clearly the case with *Ceratium hirundinella* O. F. MÜLLER, which under all circumstances is a slow-growing species, but is not submitted to grazing and to sedimentation (HEANY & TALLING 1980).

A principal restriction of the direct comparison of steady state competition experiments with phytoplankton succession in the lake lies in the fact that inoculum-independent equilibrium is achieved asymptotically with theoretically infinite time. Even if the artificial criteria used in this study to define equilibrium are considered sufficient, three to six weeks of constant environmental conditions are needed, which is extremely unprobable in temperate lakes. It might be argued that the dilution rate and hence the rate of displacement of species unable to continue growth was rather small ($0.3\,d^{-1}$). Nevertheless it was a quite realistic simulation of the natural situation, because the rates of decrease for important summer algae in Lake Constance reported by SOMMER (1981 a) vary from $0.15\,d^{-1}$ for *Ceratium hirundinella* to $0.45\,d^{-1}$

for *Aphanizomenon flos-aquae* RALFS. In contrast to the quality of the final equilibrium, the time required to achieve it and the transitional stages preceding it are highly dependent on the composition of the inoculum. This can easily be shown by the following calculation: the detection level for algae in the inoculum is roughly 0.1 cells ml^{-1}. Total algal biomass in phase II and III of the experiments varied between 1.5 and 4×10^8 $\mu m^3 \cdot ml^{-1}$. If we assume a growth rate of 1 doubling per day ($\mu = 0.69$ d^{-1}) which is rather high for the later stages of phase II, the time required to achieve 1×10^8 $\mu m^3 \cdot ml^{-1}$, a subdominant to dominant contribution to total biomass, is roughly 20 days for a species of 1000 μm^3 cell-size, 23 days for a 100 μm^3 species and 30 days for a 10 μm^3 species. If these species are present in the inoculum at 100 cells $\cdot$ ml^{-1}, which for most parts of the vegetation period is still far from being dominant, these times are reduced to 10, 13, 17 days, respectively. The shorter the periods of environmental stability, the higher the dependence of the phytoplankton species composition on its previous history. As HUTCHINSON (1967) has proposed in his fourth possible explanation to the "paradox of the plankton", phytoplankton associations are no equilibrium associations, but transitional stages between preceding associations and equilibrium associations that are never fully reached.

Summary

Natural phytoplankton from Lake Constance was exposed to competition experiments in chemostat cultures. Silicate and phosphate were chosen as potentially limiting nutrients and were offered in six different molar ratios from 4:1 to 80:1. After a start phase, in which phytoplankton development was parallel to the lake and an intermediate succession of quickly growing species a stable equilibrium was reached, that was independent from the inoculum species composition (Fig. 1). At limitation by a single nutrient competitive exclusion of all but one species occurred (4:1 *Mougeotia thylespora*, 80:1 *Synedra acus*), at double limitation two species, the green algae *Koliella spiculiformis* (P-limited) and a diatom, either *Asterionella formosa* or *Synedra acus* (Si-limited) could coexist (Fig. 2). Comparison with the lake reveiled that in agreement with the experiments, dominance of pennate diatoms is characteristic for periods of phosphorus depletion in combination with sufficient concentrations of silicate (Table 2). On the other hand the ecological niche filled by green algae in the experiments is mainly filled by Cryptophyceae in the lake. The main restriction in the application of the experimental results to real lake situations is the long time (3 to 6 weeks) of steady state conditions, that is required to obtain an equilibrium independent from inoculum. Phytoplankton in temperate lakes probably represents a transition stage between earlier associations and potential equilibria, that are never fully reached.

Zusammenfassung

Natürliches Phytoplankton aus dem Bodensee wurde für Konkurrenzversuche mit Chemostat-Kulturen eingesetzt. Silikat und Phosphat wurden als potentiell limitierende Nährstoffe ausgesucht und in 6 verschiedenen molaren Verhältnissen von 4:1 bis 80:1

angeboten. Nach einer Anfangsphase, in der die Entwicklung in den Kulturen parallel zur Entwicklung im See verlief, und einer intermediären Sukzession schnell wachsender Arten wurde ein stabiles Fließgleichgewicht erreicht, das unabhängig von der Zusammensetzung des Inokulums war (Abb. 1). Bei Wachstumslimitation durch einen Nährstoff kam es zur Verdrängung aller Arten außer einer (4:1 *Mougeotia thylespora*, 80:1 *Synedra acus*), bei Doppellimitation konnten zwei Arten, die Grünalge *Koliella spiculiformis* (P-limitiert) und eine Kieselalge, *Asterionella formosa* oder *Synedra acus* (Si-limitiert) koexistieren (Abb. 2). Der Vergleich mit dem Bodensee zeigt, daß in Übereinstimmung in den Experimenten, die Dominanz pennater Kieselalgen charakteristisch für Perioden starker Phosphataufzehrung bei gleichzeitig ausreichender Silikatversorgung ist (Tabelle 2). Andererseits wird die ökologische Nische, die in den Versuchen von den Grünalgen ausgefüllt wird, im See hauptsächlich von den Crypotophyceen eingenommen. Die Haupteinschränkung der Übertragung der Versuchsergebnisse auf den See liegt in der langen Zeit (3 bis 6 Wochen) konstanter Umweltbedingungen, die benötigt wird, um ein inokulum-unabhängiges Gleichgewicht zu erreichen. Das Phytoplankton der Seen der gemäßigten Zonen repräsentiert meistens einen Übergangszustand zwischen einer vorausgehenden Planktonassoziation und einem potentiellen Gleichgewicht, das nie voll erreicht wird.

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